Original article

Cortaderia selloana seed germination under different ecological conditions

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Abstract

Biological invasions are causing the extinction of native species and modifying ecosystem functions. Invasion success depends, among other factors, on the biological attributes of the invaders and the abiotic characteristics of the recipient community. Cortaderia selloana is a gynodioecious perennial grass native to South America which is considered invasive worldwide. It is known that seedlings of this species tolerate a wide range of environmental conditions. However, the abiotic factors that may favour its seed germination have not been studied in much detail. For this reason, we conducted an array of germination tests with different degrees of shading, soil textures and water availability. Although C. selloana usually grows in disturbed sites where light is highly available, we found that seed germination was higher under shaded conditions than under 100% light. Seed germination was higher in sandy soil textures and decreased in soils which contained increased levels of clay. Mature C. selloana plants have been reported to tolerate water stress, yet we found that the shortage of water availability constrained seed germination to approximately 60%. Overall, C. selloana seeds seem to germinate under a wide range of environmental conditions, yet germination rate can be improved under shading, high levels of sand and with high water availability.

Article history:
Received 30 June 2005
Accepted 17 September 2007
Published online

Keywords:
Alien species
Germination test
Light
Soil texture gradient
Water availability

1. Introduction

The success of introduced plant species depends largely on the biological attributes of the species (i.e. invasiveness), and on appropriate environment conditions (Lonsdale, 1999). Large seed production is a trait of many successful invaders (Baker, 1965). However, even for species that produce a great amount of viable seeds, the response of early life-history stages to the new ecological factors are crucial for the invader to succeed (Holdgate, 1986; Parker and Reichard, 1998; Shea and Chesson, 2002). Alien species are supposed to perform best in disturbed areas, right from the germination stage (Hobbs and Huenneke, 1992). Moreover, for an alien species to invade it is essential to tolerate a wide range of environmental conditions such as different degrees of shading and different soil conditions. In addition, it has been reported that invader species might have a superior response to resource pulses compared to native plants (Shea and Chesson, 2002).
2. Material and methods

2.1. Seed collection

By the end of September 2003, seeds were collected from a large population on Parc Natural dels Aiguamolls de l’Empordà (NE Spain). Ten panicles were collected from each of 25 female plants for a total of 250 panicles. We used seed from female plants placed on one layer of autoclaved filter paper. We also studied seed germination in 15 uncovered Petri dishes (n = 10) and filled with substrate from each texture. Dishes were sprayed with distilled water every day and were randomly moved every two days in order to avoid position effects and to guarantee that all dishes received the same amount of light. Germination was recorded every day and seedlings were removed. Seeds were considered as germinated when the cotyledon emerged from the soil. The effect of soil texture on the percentage of germination after 42 days was analysed using ANOVA and a subsequent Scheffé multiple-comparisons test.

2.2. Effect of shading on C. selloana germination

To test the effect of shading on seed germination we constructed three cubes of 50 × 50 × 50 cm and covered them with three different woven materials that filtered light allowing sunlight penetration of 50%, 30% and 5%. Each cube contained 15 5-cm diameter Petri dishes with 10 C. selloana seeds from female plants placed on one layer of autoclaved filter paper. We also studied seed germination in 15 uncovered 5-cm diameter Petri dishes with 10 C. selloana seeds from female plants under 100% light. The filter paper was continuously maintained saturated with distilled water and Petri dishes were randomly moved twice a week to avoid position effects and to guarantee that they were all under homogeneous conditions. Cubes were placed 1 m apart to avoid shading effects. Germination was recorded every day and germinated seeds were removed from the Petri dishes. Seeds were considered as germinated when the radicle or coleoptile was visible. Differences between the four shading treatments were analysed after 26 days by ANOVA and a subsequent Scheffé multiple-comparisons test. Percentage germination was transformed as arcsine (\(\sqrt{X} - 1\)) to meet the assumptions of homogeneity of variances.

2.3. Effect of soil texture on C. selloana germination

Seed germination was tested in a gradient of four different substrate textures that differed in their increasing percentage of sand and decreasing percentage of clay. The texture gradient was obtained by adding four progressively higher fixed quantities of sand to a soil base whose texture was coarse clay. Base soil contained 31.2% sand, 29.7% silt and 38.6% clay. The first texture was coarse clay and was obtained by mixing 2.42 kg of base soil and 0.58 kg of sand. To obtain a sandy-clay-loam texture we mixed 1.76 kg of base soil and 1.24 kg of sand. The third texture was sandy loam and it was made with 1.10 kg of base soil and 1.90 kg of sand. Finally, the fourth texture was sandy and it was made with a mixture of 0.44 kg of base soil and 2.56 kg of sand (Table 1).

Each experimentally made soil was placed in 2-litre pots that were progressively watered for 2 weeks and homogenized once they were dry. Twenty-five seeds from a pooled seed lot from 25 female plants were placed on 12 cm diameter Petri dishes (n = 10) and filled with substrate from each texture. Dishes were sprayed with distilled water every day and were randomly moved every two days in order to avoid position effects and to guarantee that all dishes received the same amount of light. Germination was recorded every day and seedlings were removed. Seeds were considered as germinated when the cotyledon emerged from the soil. The effect of soil texture on the percentage of germination after 42 days was analysed using ANOVA and a subsequent Scheffé multiple-comparisons test.

| Table 1 –– Percentage of soil fractions (ISSS criteria) for the four experimentally made textures used for C. selloana germination tests |
|---|---|---|---|---|
| Soil fractions (%) | Coarse clay | Sandy-clay loam | Sandy loam |
| Sand (2000 < D < 20 μm) | 45.0 | 60.0 | 75.0 | 90 |
| Silt (2 < D < 20 μm) | 31.1 | 22.6 | 14.1 | 5.7 |
| Clay (D < 2 μm) | 23.9 | 17.4 | 10.9 | 4.3 |

Please cite this article in press as: Doménech, R., Vià, M., Cortaderia selloana seed germination under different ecological conditions, Acta Oecol. (2007), doi:10.1016/j.actao.2007.09.004
(i) a long-duration water availability treatment in which Petri dishes were sprayed with distilled water every day in order to maintain them constantly moist, (ii) an intermediate-duration water availability treatment in which Petri dishes were sprayed with water every day during the first five weeks, (iii) a short-duration water availability treatment in which Petri dishes were sprayed with water only during the first three weeks. Each Petri dish was filled with Plantaflor® gardening soil which contained 200 mg/L of N, 180 mg/L of P₂O₅ and 230 mg/L of K₂O, and contained 25 seeds from female plants. We used gardening soil to avoid effects of local soil chemistry. There were 10 Petri dishes for each water availability combination. Petri dishes were randomly moved every two days to avoid position effects and to guarantee that they received the same amount of light. Germination was recorded every day and germinated seeds were removed. Seeds were considered as germinated when the cotyledon emerged from the soil. The effect of the duration of water availability was analysed after 2 months, when no additional seed germination under intermediate and short-duration water availability was observed, with a one-way ANOVA. Differences between water duration availabilities were calculated with a one-way ANOVA. A Scheffé test was used for pair-wise comparisons between watering treatments.

3. Results

Shade significantly increased percentage germination ($F_{3,56} = 7.57, P = 0.0002$), with about 20% fewer seeds germinating under 100% light (Scheffé test, $0.001 < P < 0.003$) than under the other light treatments, which did not differ (Fig. 1).

Percentage germination of $C. selloana$ seeds varied with soil texture ($F_{3,36} = 8.52, P = 0.0002$), increasing with increasing sand content (Fig. 2), being significantly higher in sand than in coarse clay, sandy-clay-loam and sandy-loam textures (Scheffé test, $0.0003 < P < 0.02$).

Shortage in water availability had a significant negative effect on final seed germination ($F_{2,27} = 25.35, P < 0.0001$).

Seed germination of $C. selloana$ was not completely synchronous, continuing at the short-duration water availability treatment even when seeds were not watered but Petri dishes remained moist (Fig. 3).

4. Discussion

$C. selloana$ usually invades areas where there is a high percentage of bare ground as a result of frequent disturbances (Harradine, 1991), therefore we expected high $C. selloana$ seed...
germination under high light. On the contrary, we found that shading significantly improved seed germination by 16.2%, a result which contrasts with seed germination of the conger C. jubata which is 3.3 times higher in high light than under dark conditions (Drewitz and DiTomaso, 2004). However, despite higher seed germination under dark conditions, seed germination under 100% light exposure was also very high, so this species can still benefit from disturbances, shown to be essential both by simulations (Paasas et al., 2006) and field experiments (Doménech and Vilà, 2006) for the persistence and expansion of this species.

Previous germination tests proved that C. selloana seeds can germinate in a wide variety of soil types such as dune scrub, maritime chaparral, grassland and wetland soil (Lambrinos, 2002) though seedling establishment is said to require sandy soils (Bossard et al., 2000). This is consistent with our findings that sandy soil texture significantly enhanced C. selloana seed germination. Furthermore, a field survey conducted in ruderal and non-ruderal habitats across a Mediterranean coastal strip revealed that C. selloana was invading habitats whose soil had more than 60% sand (Doménech, 2005). Conversely, we found that this species also germinated in soils which contained lower percentages of sand, showing that germination in C. selloana can proceed in wide range of soil textures.

We also suspected that C. selloana seed germination would not be severely affected by water availability, as it had been previously found that C. selloana mature plants can resist moderate and severe water stress (Bossard et al., 2000). In addition, greenhouse experiments conducted with seedlings have revealed that C. selloana seedlings are more drought tolerant than those of Festuca arundinacea and Brachypodium phoenicoides, two co-existing native species of the same functional group (Doménech, 2005). We found that seed germination of C. selloana did not cease completely after stopping watering, and that some seeds remained viable in the Petri dish for several weeks before germinating, suggesting that this species has a staggered germination strategy.

Overall, C. selloana seed germination was increased under shaded conditions, in sandy soils and when water was highly available for a long time. However, the germination requirements of this species were not very stringent, so the invasive success of C. selloana may be partially attributable to a great capacity to germinate under a wide range of ecological conditions. Moreover, it must be considered that C. selloana mature plants produce a high quantity of viable seeds (Doménech, 2005) which the wind disperses widely and have the potential to invade a wide variety of new environments if they find suitable germination conditions.

Acknowledgements

We thank J. Shykoff and two anonymous referees for comments on an earlier draft of this paper and L. Marco for helping to maintain the germination tests. Funding was provided by the REN2000-0361/GLO project from the Ministerio de Ciencia y Tecnología.

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